THE FIRST RECORD OF MULTIPLE ALLELOMORPHISM IN A BRITISH BUTTERFLY: *COENONYMPHA TULLIA* (MÜLLER) SSP. *POLYDAMA* (HAWORTH) (LEPIDOPTERA: SATYRIDAE)

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ABSTRACT

Breeding work (carried out since 1988 by Martin White) with two unnamed ground colour aberrations of the Large Heath butterfly *Coenonympha tullia* (Müller) has revealed the first recorded instance of multiple allelomorphism in a British butterfly. Both colour forms have proven recessive to type. They show grey and orange ground colour, respectively. When the two aberrations are crossed together the F_1 generation contains 100% butterflies which exhibit a shimmering or translucent effect on an otherwise typically coloured background. Back crossing these hybrids with (typically coloured) individuals that were heterozygous for either grey or orange aberrations, produces an F_2 generation containing 50% typical: 25% either grey or orange: 25% translucent. This 2:1:1 ratio demonstrates that the grey and orange aberrations involve the same gene locus.

INTRODUCTION

Genes occur in pairs in Lepidoptera, one inherited from each parent. Each gene of a pair occurs at a particular location ('the locus') on its particular chromosome. Either gene in a pair may be typical or it may be a mutation. The alternative forms of a gene at a locus are termed alleles (Majerus, 1998). If a mutation occurs in a gene which codes for an element of the adult wing pattern or colouring, then the adult insect may display aberrant patterning or coloration. For example, many melanic forms of British moths are due to the existence of a mutant (frequently dominant) allele. However, a gene may not necessarily have just two alternative forms. In some cases there may be several alternative forms of a gene that may lead to various alternative wing patterns or colours. These alternative mutations are termed multiple alleles and the condition is called multiple allelomorphism (Majerus, 1998).

The most famous and well-studied example in the Lepidoptera occurs in the widespread African Mocker Swallowtail butterfly *Papilio dardanus* (Brown). The adult male has a black and yellow pattern, but the female occurs in a number of quite different forms, each one a mimic of an unpalatable model butterfly unique to its region. Each of these female forms is controlled by one of ten alleles at one locus (Ford, 1964; Nijhout, 1991; Majerus, 1998).

Multiple allelomorphism is also known from British moths, for example in the Pale Brindled Beauty *Phigalia pilosaria* (D. & S.). In this case the typical pale form, the fully melanic form *monacharia* (Staud.) and the intermediate form *pedaria* are all controlled by different versions of the same gene (Majerus, 1998). The condition has also been recorded in the tortricid *Acleris comariana* (Lienig & Zeller) (Ford, 1964; Majerus, 1998).

Despite British butterflies being such a well-studied group, multiple allelomorphism has not previously been recorded. In 1945, the geneticist E.B. Ford wrote 'The

phenomenon is of much interest from evolutionary and other points of view, and when found in a British butterfly, the fact should be published'.

Multiple allelomorphism in *Coenonympha tullia*

This involves two very local colour forms which have not previously been named or described. They have been found in an isolated population on the Humberhead Levels (an area of lowland peat stretching from Goole Moors in North Lincolnshire, through South Yorkshire east of Doncaster, to Gringley Carr in Nottinghamshire). They are best described as butterflies in which the wing markings are unaffected, but which lack the typical 'cinnamon' ground colour of typical Humberhead specimens, centred on Munsell colour co-ordinates 7.5YR 5.5/7 (Munsell, 1994). (Munsell co-ordinates provide a standardised numerical reference system for identifying and comparing colours to a high degree of precision.)

One of the newly described colour forms has been captured on a few occasions in the past, but the other may be entirely new. As regards the Humberhead Levels, it is possible that this new aberration mutated or evolved in the same 'colony-enclave', together with a number of other distinctive ground colour forms, sometime after 1901 when a major drainage scheme isolated their parent sub-population from the main Humberhead Levels meta-population. Neither of the two forms, described below, nor indeed any of the other forms, have so far been observed or recorded from the main, much larger, ancestral population despite the enthusiastic activities of naturalists studying the species here for well over a hundred years. The genetic inheritance of the other (concomitantly occurring) forms remain unstudied. Further breeding work will therefore be needed to determine whether these are also controlled by separately mutated alleles at the same locus as the two forms described below.

The two ground colour forms

ab. *lunaris*

In this aberration the cinnamon ground colour is replaced by shades of grey (Plate 3 Figs 5–8 compared to typical specimens Figs 1–4). Three specimens of this aberration are held in the National Butterfly Collection at the Natural History Museum, London. Their data are as follows: Grange, 1904, W. Feather; Witherslack, 1905, F.W. Frohawk and Aviemore, 1915, S.G. Castle Russell. As regards the Humberhead Levels population, the earliest known example was a perfect male first noticed by Malcolm Simpson and subsequently captured by another observer on 8 July 1982. Between this date and 1998 a further 48 individuals were recorded or captured at an approximate ratio of 1 in 400 butterflies observed. Most of these original grey examples were, or have been, closely examined and in all but two cases scored a near monochromatic appearance (centred on Munsell: 10YR 5/3). The two remaining specimens, both male, exhibited a yellowish-green tint (10YR 5.5/4). The second of these 'yellowish-green' grey males (captured 27 June 1996) was captive-paired with reared virgin females and gave rise to a large part of the stock for this breeding programme.

A cross between a grey aberration and a typically coloured homozygote produces an F_1 generation all typical in appearance (all being heterozygotes) and an F_2 that contains 75% typical butterflies: 25% grey examples. This represents the classic Mendelian ratio for a recessive form of 1 typical homozygote: 2 typical heterozygote: 1 aberration, thereby proving that the grey aberration is recessive to type. Extensive breeding work has revealed considerable variation in the expression of the grey

aberration, from pure monochromatic grey individuals without a trace of typical cinnamon colour, through to those of a yellowish-green tint. This range currently models exactly the same shape in visible 'colourspace' (in terms of hue (wavelength), brightness (luminosity) and chroma (saturation)) as the corresponding range of variation and relative abundance in typical butterflies (including sexual dimorphism). This is perhaps to be expected, as the same set of modifier genes will be involved in controlling the expression of the ground colour in both the aberrant and typical butterflies. There is still, however, an obvious gap between the range of colour displayed by the grey butterflies and their typical counterparts.

ab. *ejecta*

This is the most striking colour form of the species yet discovered on the Levels. It is best described as having typical markings but a reduction in melanin pigments. The result is an orange butterfly with paler markings replacing the normally deep black rings around the eyespots (Plate 3 Figs 9–12). By comparison with the current colour dynamics of the grey form, far less variation has, so far, appeared within this aberration. Before 1994, variation in its wing coloration corresponded to just a single point in visible colourspace at 7.5YR 6/10, but now extends from here, through a series of intermediates, to approximately 7.7YR 5.5/9, contiguous with examples at the brightest extreme of the typical range.

The earliest known specimen of this form was a male captured by Reg Carter on 28 June 1981. Between this date and 1998 a further nine authenticated examples were recorded at an approximate ratio of 1 in 2000 individuals observed. Most of these aberrations, especially those taken before 1986, showed minor signs of wing-crumpling. However a perfect orange male, captured on 17 June 1999, was mated with home-reared virgin females, giving rise to most of the stock for this experiment. Subsequent back-crossings increased stock vigour and proved that this orange aberration is recessive to the type.

The release of progeny resulting from both *lunaris* and *ejecta* stocks between 1999 and 2003 by Martin White (under a licence issued by Butterfly Conservation) has increased the abundance of these rare aberrations in the wild and helped re-establish a new Humberhead Levels colony. As a result the yellowish-green forms of *lunaris* have now replaced the monochromatic form as the most commonly encountered grey 'sub-form' found in the wild.

Crossing the two forms

It was found that when the grey *lunaris* was crossed with the orange *ejecta* they gave rise to an F_1 generation made up entirely of a new (provisionally named) 'Rosy' aberration. The variability in hue, brightness and chroma of this aberration was exactly the same as that found in typical butterflies, but all 'Rosy' aberrations were characterised by a supplementary translucent or shimmering effect to varying degrees.

When one of these aberrations was back-crossed to a heterozygote of either *lunaris* or *ejecta* (typical in appearance due to the recessive nature of the aberrant alleles) the offspring closely followed the ratios of 50% typical specimens (all heterozygotes): 25% either *lunaris* or *ejecta* (depending on which heterozygote was introduced into the back-cross): 25% Rosy aberrations. This ratio of 2:1:1 was exactly as would be expected if *lunaris* and *ejecta* were due to mutations of the same gene. This demonstrates that these aberrations are the result of multiple allelomorphism.

Legend for Plate 3:

Allelomorphism in the Large Heath

1
typical male
upperside

2
typical female
upperside

3
typical male
underside

4
typical female
underside

5
male ab. *lunaris*
upperside

6
female ab. *lunaris*
upperside

7
male ab. *lunaris*
underside

8
female ab. *lunaris*
underside

9
male ab. *ejecta*
upperside

10
female ab. *ejecta*
upperside

11
male ab. *ejecta*
underside

12
female ab. *ejecta*
underside

All specimens bred by M.C.White
Specimens in collection of R. Barrington

Allelomorphism in the Large Heath *Coenonympha tullia* ssp. *polydama*